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Transpiration and dry matter allocation in the angiosperm root parasite *Cynomorium coccineum* L. and two of its halophytic hosts

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Abstract

The angiosperm root parasite *Cynomorium coccineum* and the halophytic hosts *Limonium delicatulum* and *Arthrocnemum glaucum* were investigated under natural conditions in a Mediterranean salt marsh in March 1992. The diurnal transpiration rate of the parasite was low and parallel to the climatic factors. The non-infected plants showed higher transpiration rates than the parasite and its hosts. Compared to the non-infected plants, it is apparent that the perennial herb *L. delicatulum* is more sensitive to infection since its reduction in the fresh and dry mass was higher than that found in *A. glaucum*.

Introduction

Cynomorium coccineum L. is a perennial angiosperm holoparasite (obligate parasite) on roots of halophytes in the Mediterranean coastal salt marshes (Täckholm 1974, Fahmy 1986, 1992). There have been few studies on the ecology and biology of *C. coccineum*. These reports dealt mainly with taxonomy and anatomy of the plant (Weddell 1858) or anatomy and fine structure of infection and the ionic composition of the hosts and the parasite (Fahmy 1986). Based on the assumption that the stomata on the perianth segments of the flowers on the aboveground inflorescence are non-functioning, and on the extremely low relative conducting area of the parasite inflorescence [6×10^{-3} mm^2 g^{-1}(f.m.)] compared to the hosts [0.43 - 0.85 mm^2 g^{-1} (f.m.)], it has been suggested that the parasite has low transpiration rate (Fahmy 1992). The aim of the present paper was to verify this suggestion and to investigate the magnitude of transpiration of the host plants compared to the parasite as well as the non-infected plants. The fresh and dry mass of the host-parasite associations and the non-infected plants have also been investigated.

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Materials and methods

Site characteristics and plant material: The study site of *Cynomorium coccineum* and its associating species is a part of a Mediterranean coastal salt marsh located about 56 km west of Alexandria. It extends 5 km to the west and is 0.2 km broad. It is delimited to the north by a coastal belt of sand dunes with a high calcium carbonate content. The climate is arid with mild winter and warm summer. The annual rainfall is variable, ranging from 87 to 246 mm (Abd El-Rahman *et al.* 1966). The air temperature ranged between a mean of 13.6 °C in February and 27 °C in August. *Cynomorium coccineum* and its associating halophytic species grow in saline soil with shallow water table (Fahmy 1986). The total soluble salt of the soil ranged from 9.28 % of dry soil mass in the surface layer to 1.38 % in the deeper layers.

The plant body of *C. coccineum* is a subterranean rhizome with the only annual aboveground flowering stalk (Fig. 1) of numerous unisexual and bisexual minute flowers mixed together (Jafri 1977). The rhizome carries short and long haustoria (Fahmy 1992). Many stomata are present on the perianth segments and bracts of the aboveground inflorescence of the parasite (Pirotta and Longo 1899, Fahmy 1986).

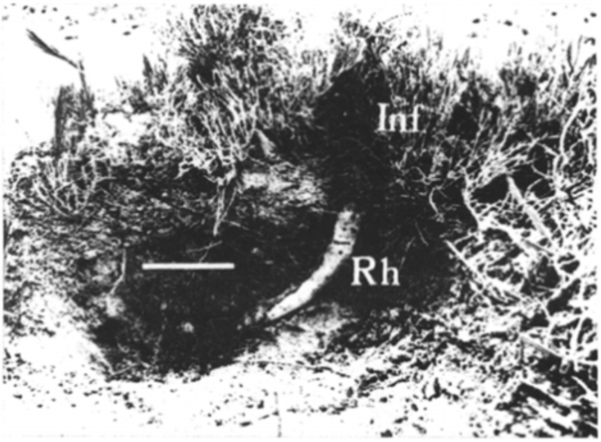

Fig. 1. An individual root parasite *Cynomorium coccineum* associating different halophytic species in the salt marsh. The soil has been excavated to expose the underground rhizome (Rh) of the parasite which was peeled off for contrast in the photograph (Inf - aboveground inflorescence). Scale marker = 12 cm.

Transpiration: Since the parasite is able to infect more than one individual host at the same time (Fahmy 1986), it has been considered that the individuals associating and growing in the vicinity of the parasite, were the possible infected plants. This aboveground inspection has been achieved one day before the transpiration experiment. On the following day, the hosts have been confirmed by the ground excavations to expose the roots attached to the parasite.

For the transpiration measurements, the rapid weighing method of the detached parts cut from the fully developed plants of the hosts and the non-infected plants was used. Measurements of transpiration and climatic factors were carried out on 14 March 1992 at intervals of 2 h for a period extending from before sunrise at 06.00 to after sunset at 20.00 (local time).

Fresh and dry mass and water content: The fresh mass of the parasite as well as that of transpiring and the non-transpiring parts (senescent or dry parts) of the hosts and the non-infected plants were determined. The plant material was oven-dried at 70 °C for 48 h. Water content was calculated and expressed as percentage of fresh mass.

Statistical analysis: The data of climatic factors are the arithmetic means of three replicates. The differences in transpiration rates at each time of the day were analysed by the analysis of variance (Snedecor and Cochran 1967).

Results

Transpiration: In general, the transpiration rate of the parasite, the hosts and the non-infected plants could be distinguished into three levels. The highest level was exhibited by the salt secreting halophyte, *L. delicatulum* and the lowest level was demonstrated by the parasite (Fig. 2). The intermediate level was shown by the stem succulent *A. glaucum.*

Table 1. Diurnal variations of climatic factors in the study area on 14 March 1991.

Day time [h]	Air temperature [°C]	Evaporation [μm s^{-1}]	VPD [kPa]	Wind speed [m s^{-1}]
06.00	15		0.1	0
08.00	19	0.01	0.2	0.4
10.00	21	0.02	0.3	0.7
12.00	23	0.10	0.6	1.2
14.00	22	0.19	0.7	1.8
16.00	19	0.10	0.5	1.5
18.00	17	0.07	0.3	2.0
20.00	16	0.04	0.2	0.7

The maximum transpiration rates of *L. delicatulum* and *A. glaucum* were observed earlier than those of the corresponding climatic factors. These were obtained at 10.00 *i.e.*, 4 h earlier than those of the maximum VPD. and evaporation rates (Table 1). The host plants of *L. delicatulum* and *A. glaucum* showed significant lower transpiration rates than the non-infected plants (Fig. 2). On the other hand, the maximum transpiration rates of *C. coccineum* were observed at 12.00 and 14.00 when the climatic factors attained their maximum.

The daily mean transpiration rates in the different species were higher in the hosts and the non-infected plants of *L. delicatulum* (Table 2) than those of *A. glaucum*. The parasite showed the lowest daily mean transpiration rate.

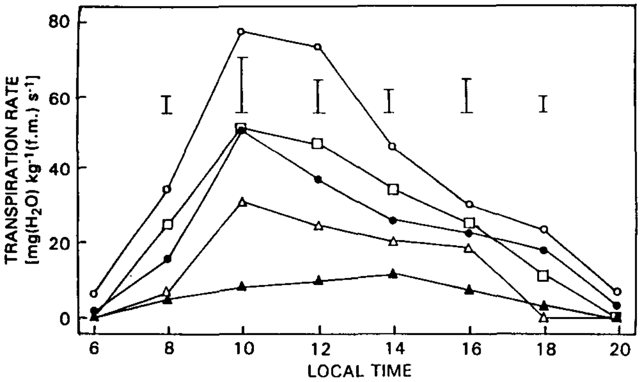

Fig. 2. Diurnal variations of transpiration rates under natural conditions in the salt marsh on 14 March 1991. The vertical line bars are the least significant differences (LSD) at 5 % probability level between the means. The LSD values at 06.00 and at 20.00 are 2.8 and 5.0 mg(H_2O) kg^{-1}(f.m) s^{-1}, respectively. *Limonium delicatulum*, host - *closed circles*; *Arthrocnemum glaucum*, host - *open triangles*; the non-infected plants of *Limonium* and *Arthrocnemum* - *open circles* and *open squares*, respectively; the root parasite *C. coccineum* - *closed triangles*.

Table 2. Transpiration, fresh and dry masses and the water content of the root parasite *Cynomorium coccineum* and its halophytic hosts and the non-infected plants of *Limonium delicatulum* and *Arthrocnemum glaucum* growing under natural conditions in the salt marsh in March 1991. Each value is an average of 5 measurements ± standard deviation. P - parasite, NI - non-infected plant, H - host plant.

	Cynomorium coccineum	*Limonium delicatulum*		*Arthrocnemum glaucum*	
	P	NI	H	NI	H
transpiration rate [mg(H_2O) kg^{-1}(f.m.) s^{-1}]	5.3 ± 0.6	37.8 ± 4.7	21.9 ± 1.9	24.4 ± 2.8	12.8 ± 1.1
Sum of transpiration [g(H_2O) plant^{-1} d^{-1})]	9.9 ± 1.5	140.5 ± 14.0	26.3 ± 2.1	1123.2 ± 59.0	380.8 ± 31.0
Fresh mass of tranpiring parts [g]	64.4 ± 6.4*	129.6 ± 29.0	41.6 ± 6.4	1600.0 ± 102	1032.0 ± 91.0
Dry mass of transpiring parts [g]	19.3 ± 2.0	38.0 ± 1.8	15.2 ± 1.6	352.0 ± 40.0	289.0 ± 26.0
Water content [% (f.m.)]	70.0 ± 8.5	70.7 ± 3.4	63.5 ± 3.4	78.2 ± 2.5	72.1 ± 1.4
Dry mass of non-tranpirating parts [g]	-	5.1 ± 0.7	9.3 ± 1.2	51.0 ± 3.4	98.0 ± 4.7
Tranpirating to non-transpirating parts ratio	-	7.5 ± 2.0	1.6 ± 1.1	31.4 ± 5.5	2.9 ± 1.4

*inflorescence only

The hosts showed lower values of total daily transpiration than the non-infected plants. It is worthy to indicate that, despite the non-infected *L. delicatulum* plants had the highest transpiration rate (both diurnal and daily means), their total daily transpiration was lower than the host and the non-infected individuals of *A. glaucum* (Table 2). This is attributed to the lower values of fresh and dry mass of *L. delicatulum* compared to *A. glaucum.*

Fresh and dry mass and water content: Both the fresh and the dry mass of the hosts were lower than the non-infected individuals. The fresh and dry masses of the parasite (inflorescence + underground rhizome) were higher than of the hosts and the non-infected plants of *L. delicatulum* and both of them were lower than those *A. glaucum* (Table 2).

The water content of the host plants was always lower than the non-infected plants. The dry mass of the decorticated shoots of *A. glaucum* or the dead leaves of *L. delicatulum* hosts were higher than those of the non-infected plants. This is manifested by the ratio of the dry mass of the transpiring parts and non-transpiring parts of the non-infected and the host plants. The ratio was 31.4 in the non-infected plants of *A. glaucum* and was 2.9 in the host plants (Table 2).

Discussion

Transpiration: The root parasite *C. coccineum* seems to be a saver of water, its aboveground inflorescence showed maximum transpiration rate at 14.00 which was from 0.44 to 0.56 times less than that of its hosts *A. glaucum* and *L. delicatulum* at similar climatic conditions. At that time of the day the transpiration rates of the hosts and the non-infected plants were lower than their early maxima attained at 10.00. This indicates stomatal control in both the hosts and the non-infected plants. Since the stomata on the perianth segments and bracts of *C. coccineum* inflorescence do not show diurnal movements (Fahmy, unpublished data) and whereas their aperture is narrow (Fahmy 1992), the result will be a low stomatal conductance to water vapour. A high stomatal conductance occurs only if the stomata are functioning as in the hemiparasites (*Loranthus, Viscum, Pthirusa maritima, etc.*) which rely upon their hosts for a source of water and minerals but produce to a certain extent their own supply of assimilate *via* carbon fixation (Goldstein *et al.* 1989). Being a holoparasite with low transpiration rate, *C. coccineum* is again different from other holoparasitic flowering plants as *Orobanche* species which showed active water secretion *via* the glandular capitate trichomes on the inflorescence. In the *Orobanche* species the stomata are reduced and non-functioning (Rakhimov 1967). Though, in *C. coccineum*, the absence of a known mechanism of water secretion during the daytime, together with the assumption that the guard cells are non-functioning (Fahmy 1992), may account for its low diurnal transpiration rate which is a possible but not a common exception among the parasitic flowering plants. Härtel (1941) found that some hemiparasites have much lower rates of transpiration than their hosts. The osmotic gradients between *C. coccineum* and its hosts *A. glaucum* and *L. delicatulum* (Fahmy 1992) induced water transport in the direction to the parasite.

The low transpiration rate of the host plants compared to the non-infected ones is mainly due to the continuous tapping of their water and solutes by the parasite. Thus the water uptake by the host roots may be insufficient to replace the normal loss due to the tapping by the parasite as well as by transpiration.

Fresh and dry mass and water content: It is apparent that *L. delicatulum* is more sensitive to infection than *A. glaucum* since the fresh and dry mass of the hosts of the former were 68 and 60% lower than those of the non-infected plants. The small biomass of *L. delicatulum* together with its relatively higher transpiration rate and less negative osmotic potential than the other host *A. glaucum* (Fahmy 1992) are among the reasons for its sensitivity to infection by *C. coccineum*. The reduction of fresh and dry mass has been recorded in the hosts of the holoparasitic flowering plants like *Orobanche* (Singh *et al.* 1971).

The low ratio of the dry mass of the transpiring to the non-transpiring parts of the hosts compared to the higher ratio in the non-infected plants is a direct consequence of infection. Appearance of some visual symptoms of the hosts such as increase of stem decortication of *A. glaucum* or leaf senescence followed by death in *L. delicatulum* will enable the hosts to reduce their water expenditure.

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